Species–area and species–individual relationships for tropical trees: a comparison of three 50-ha plots

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Summary

1 Species–accumulation curves for woody plants were calculated in three tropical forests, based on fully mapped 50-ha plots in wet, old-growth forest in Peninsular Malaysia, in moist, old-growth forest in central Panama, and in dry, previously logged forest in southern India. A total of 610 000 stems were identified to species and mapped to < 1 m accuracy. Mean species number and stem number were calculated in quadrats as small as 5 m × 5 m to as large as 1000 m × 500 m, for a variety of stem sizes above 10 mm in diameter. Species–area curves were generated by plotting species number as a function of quadrat size; species–individual curves were generated from the same data, but using stem number as the independent variable rather than area.

2 Species–area curves had different forms for stems of different diameters, but species–individual curves were nearly independent of diameter class. With < 10^4 stems, species–individual curves were concave downward on log–log plots, with curves from different forests diverging, but beyond about 10^4 stems, the log–log curves became nearly linear, with all three sites having a similar slope. This indicates an asymptotic difference in richness between forests: the Malaysian site had 2.7 times as many species as Panama, which in turn was 3.3 times as rich as India.

3 Other details of the species–accumulation relationship were remarkably similar between the three sites. Rectangular quadrats had 5–27% more species than square quadrats of the same area, with longer and narrower quadrats increasingly diverse. Random samples of stems drawn from the entire 50 ha had 10–30% more species than square quadrats with the same number of stems. At both Pasoh and BCI, but not Mudumalai, species richness was slightly higher among intermediate-sized stems (50–100 mm in diameter) than in either smaller or larger sizes. These patterns reflect aggregated distributions of individual species, plus weak density-dependent forces that tend to smooth the species abundance distribution and 'loosen' aggregations as stems grow.

4 The results provide support for the view that within each tree community, many species have their abundance and distribution guided more by random drift than deterministic interactions. The drift model predicts that the species–accumulation curve will have a declining slope on a log–log plot, reaching a slope of 0.1 in about 50 ha. No other model of community structure can make such a precise prediction.

5 The results demonstrate that diversity studies based on different stem diameters can be compared by sampling identical numbers of stems. Moreover, they indicate that stem counts < 1000 in tropical forests will underestimate the percentage difference in species richness between two diverse sites. Fortunately, standard diversity indices (Fisher's α, Shannon–Wiener) captured diversity differences in small stem samples more effectively than raw species richness, but both were sample size dependent. Two nonparametric richness estimators (Chao, jackknife) performed poorly, greatly underestimating true species richness.

Keywords: diversity, tropical forest, species–area curve, species–individual curve

Introduction

Species–area and species–individual curves have been central to community ecology for decades (Fisher *et al.* 1943; Preston 1948, 1962; MacArthur & Wilson 1967). They are a fundamental component of conservation biology and are frequently used to formulate recommendations about species preservation and to predict extinction rates caused by habitat destruction (Diamond 1975; Schafer 1990; Pimm *et al.* 1995). Despite widespread attention from field ecologists and mathematical biologists, species–area analysis is largely empirical: the theoretical basis of the species–area curve is not well understood (Simberloff 1976; Angermeier & Schlosser 1989; Kelly *et al.* 1989; Kohn & Walsh 1994; Hubbell 1995, in press). Even the empirical form of species–area and species–individual relationships is debated at length (Connor & McCoy 1979).

Trees are a useful subject for analyses of such relationships, because they are easy to locate precisely and to count, and tropical trees are an especially interesting subject because they are so diverse. Many studies of local diversity of tropical trees exist, and there is a great deal of interest in patterns and processes relating to tropical forest diversity (Gentry 1988; Wright 1992; Phillips *et al.* 1994; Phillips & Gentry 1994; Valencia *et al.* 1994; Condit 1995). Nevertheless, there are few detailed analyses of species–area and species–individual relationships from tropical forests.

Here we present a thorough documentation of how species richness increases with the area censused or with the number of trees censused, using data from three 50-ha plots in three different forest types. One plot is in aseasonal, highly diverse forest in peninsular Malaysia (Manokaran *et al.* 1992), the second in seasonal, moderately diverse forest in Panama (Hubbell & Foster 1983; Condit *et al.* 1992b), and the third in seasonal, dry, low-diversity forest in southern India (Sukumar *et al.* 1992). Each plot was censused in exactly the same way: a 1-km × 0.5-km region was mapped, and all trees ≥ 10 mm in stem diameter were identified and precisely located within it. The plots form part of an international network of 12 large-scale forest dynamics plots now underway (Condit 1995). With this unique database, we seek general answers about species–area patterns of tropical forests. What is the form of the species–area and species–individual relationship? How does it change when different stem sizes are included? Does the shape of a quadrat affect the number of species found within, given constant area? Does the number of individuals within a constant area affect the number of species? And, most generally, what theories of community structure are consistent with observed species–accumulation patterns?

Materials and methods

STUDY SITES

The plot in Malaysia is in the Pasoh Forest Reserve in the centre of the Malay peninsula, 140 km southeast of Kuala Lumpur. The reserve is a 2000-ha remnant of old-growth forest connected to a larger production forest, dominated by Dipterocarpaceae and classified as red meranti-keruing by Wyatt-Smith (1987). Rainfall is 2000 mm per year and relatively aseasonal, with every month averaging more than 100 mm (Kochummen *et al.* 1990). The canopy is evergreen. The forest is on level terrain, with topographic variation of 25 m in 50 ha. There are 817 species and 335 000 stems ≥ 10 mm in diameter in the 50-ha plot (Manokaran *et al.* 1992).

The plot on Barro Colorado Island in the Panama Canal is also in rich, old-growth tropical forest (except for two of the 50 ha, which were cleared < 100 years ago), dominated by Leguminosae and Bombacaceae. Rainfall is highly seasonal, with a strong 4-month dry season from December through April, but the yearly total of 2500 mm exceeds that at Pasoh (Leigh *et al.* 1982). About 18% of the canopy is deciduous (Condit *et al.* 1996). The 50-ha plot is on mainly level terrain on the island's summit, with 28 m of vertical variation. The forest at BCI is structurally quite like the one at Pasoh, with 244 000 stems ≥ 10 mm in diameter in 50 ha, but there are only 303 species in the plot (Condit *et al.* 1992b).

The third plot is in the Mudumalai Game Reserve in the state of Tamil Nadu, about 250 km south-west of Bangalore, India (Sukumar *et al.* 1992). This is a dry, deciduous forest, dominated by teak (*Tectona grandis*, Verbenaceae), Lythraceae, and Combretaceae, and was subjected to logging until the 1960s. Rainfall is 1200 mm per year, with a December–May dry season during which most canopy trees lose their leaves. The reserve is on a rolling plateau just north of the Nilgiri Hills, and topographic variation within the plot is 129 m. Structurally, the forest at Mudumalai is very different from the other two 50-ha plots: there are just 26 000 stems in 50 ha, and grasses dominate the understorey, but large trees form a nearly complete canopy. Fires are common, and elephants play a major role as browsers on young trees and shrubs. There are only 71 species in 50 ha, less than one-tenth the richness at Pasoh.

CENSUS METHODS

All free-standing, woody stems ≥ 10 mm diameter at breast height (d.b.h.) were identified, tagged, and mapped to the nearest metre (Hubbell & Foster 1983; Manokaran *et al.* 1990; Sukumar *et al.* 1992; Condit *et al.* 1995). The diameter of each stem was measured 1.3 m above the ground unless there were irregularities

in the trunk there, in which case the measurement was taken at the nearest lower point where the stem was cylindrical, or above the buttresses on large trunks. Diameters at breast height were measured with callipers and recorded to the nearest millimetre. Trees with multiple stems connected near the ground were counted as single individuals and assigned the d.b.h. of the largest stem (d.b.h. of the secondary stems was recorded but not used in this analysis). The Pasoh 50-ha plot was fully censused from 1986 to 1989, then again in 1990; we use data from the first census here. BCI censuses were carried out in 1981–83, 1985, 1990 and 1995 (Hubbell & Foster 1983, 1986, 1992; Condit et al. 1992a,b); here we use 1990 data. Mudumalai was censused completely in 1987 and 1991; we use 1987 data here.

SPECIES–AREA CURVES

To generate species–area curves, the entire 50-ha plot was divided into nonoverlapping square or rectangular quadrats, and the number of species present in each tallied. For example, the plot can be split into 1250 20-m × 20-m quadrats. Square quadrats of the following dimensions were used: 5, 10, 20, 25, 31.6 (to give 0.1 ha), 40, 50, 100, 150, 200, 250 and 500 m. In cases where the dimension of the whole plot (500 m × 1000 m) did not divide evenly into the size of the quadrat, the northern edge or eastern edge of the plot was left out. For example, with 150-m × 150-m quadrats, only 450 m × 900 m of the plot could be used, so the northern 50 m and the eastern 100 m were omitted. The mean number of species in each size quadrat gave a species–area curve for square quadrats. The same approach was used for rectangular quadrats: we divided the plot into adjacent, nonoverlapping rectangles of 200 m × 2 m, 400 m × 4 m, 500 m × 5 m and 1000 m × 10 m, thus maintaining a constant shape, plus 500 m × 20 m, 1000 m × 1 m, and 1000 m × 500 m (full plot); in each, the long dimension was parallel to the 1000-m axis of the full plot. Long, thin quadrats were chosen to contrast with squares and to match the shape of frequently used transects (Boom 1986; Gentry 1988).

SPECIES–INDIVIDUAL CURVES

Species–individual curves were constructed exactly as were species–area curves, but instead of area on the horizontal axis we used the mean number of individuals in quadrats of each area. We also evaluated species–individual curves within quadrats of a single area, for example, species number vs. stem number from the 50 one-hectare squares. This was repeated for square quadrats 20, 25, 40 and 50 m on a side, and regressions of species number vs. the logarithm of individual number performed. This was done for stems ⩾ 10 mm d.b.h. but not the other d.b.h. classes (see d.b.h. classes).

Species–individual curves were also extended to areas much larger than 50 ha, based on available species counts in regional floras. There are an estimated 3197 species of trees and shrubs in the 131 000 km² of Peninsular Malaysia (Kochummen et al. 1992). On BCI, Croat (1978) lists 450 species of trees and shrubs, and we found a further 17 in the 50-ha plot. In the Panama Canal Area, with 1259 km² of land, there are 855 native trees and shrubs, while in the entire nation of Panama, with 77 000 km², there are 2870 species (these are based on the computerized flora of Panama released by the Missouri Botanical Garden (see D'Arcy 1987a,b), updated by R.B.F.). At Mudumalai, one of us (R.S.) counted 229 tree and shrub species in the plant checklist, which covers the 32 100-ha sanctuary. To estimate the number of individuals in the larger areas, we applied the density of plants ⩾ 10 mm d.b.h. within the 50-ha plots, thus assuming that the entire region was covered with forest of similar structure and also assuming that counts of 'trees and shrubs' include all species ⩾ 10 mm d.b.h. Obviously, these estimates are crude, but slopes on a double-log plot are not that sensitive to moderate errors. We calculated log–log slopes for species–individual curves using adjacent points – successively larger samples – on the graphs.

COMPARISON TO OTHER METHODS

There are two main approaches to constructing species–area curves which differ in the order in which quadrats (or individuals) are accumulated (Palmer 1990). One is to use a nested series of expanding quadrats. With this approach, geographical integrity is maintained, since quadrats are added in geographical order (the order is obvious in a linear series of quadrats, less obvious but still definable in a rectangular plot). A large number of nested series can be recalculated from one dataset, starting from a different point each time, to yield a mean accumulation curve. Our approach is effectively identical to this, since we calculated the number of species in rectangular quadrats of expanding size. Our technique is much easier, though, and it fully samples the plots while avoiding nonindependence of repeated curves (multiple random nested series might have partially overlapping quadrats of a given area; in our method, quadrats of a given area never overlap).

The alternative approach is to add individuals or quadrats in random order from across the whole plot (Palmer 1990; Colwell & Coddington 1994). Geographical integrity is lost, since the second quadrat (or individual) added may be far away from the first. Fortunately, it is possible to calculate analytically a curve based on random stem order, so it is not necessary to use a sampling approach. We describe this method below as the Hurlbert (1971) formulation of 'expected species number'. The alternative of randomizing quadrat order maintains geographical

integrity within the smallest quadrat area but loses integrity at larger areas.

There are drawbacks to the randomization approach. Most importantly, the species–accumulation curve will depend on the size of the area sampled, and thus is not comparable across sites. For example, with a 1-ha plot at one site and a 10-ha plot at another, a curve based on the nested approach from the former would be strictly comparable to the first hectare of a curve from the latter site; this would not be true of the randomization approach. The second drawback is that the randomization method does not actually report the number of species present in a given contiguous area, instead, it gives the number of species found in small, scattered quadrats, which is not a very useful number. The method we use here reports the actual average of species counts within quadrats of various sizes.

D.B.H. CLASSES

Species–area and species–individual curves were calculated separately for all stems $\geqslant$ each of the following d.b.h. cut-offs: 10 mm (all stems in each census), 20, 25, 31.8 (giving a circumference of 100 mm), 50, 100, 200, 300, 400 and 600 mm. These cut-offs were designed to match most other forest surveys, allowing direct comparisons. These are overlapping classes, that is, individuals $\geqslant$ 100 mm d.b.h. are included within the group $\geqslant$ 10 mm d.b.h. This approach was chosen to permit direct comparison with other studies of tropical forest, which nearly always count all stems above one of these limits. It has the drawback, however, that the d.b.h. classes are not independent of one another. Thus, in order to compare species diversity in different d.b.h. classes, we repeated calculations using nonoverlapping d.b.h. classes: 10–29, 30–49, 50–69, 70–99, 100–149, 150–199, 200–299, 300–499 and $\geqslant$ 500 mm.

INDICES OF DIVERSITY

We calculated four commonly used indices of diversity: Fisher's α, Simpson's index, the Shannon–Wiener index, and the index of dominance. Fisher's α is defined by

$$S = \alpha \ln \left(1 + \frac{N}{\alpha} \right) \tag{1}$$

where S = species number, N = individual number, ln means the natural logarithm, and α is the sole parameter (Fisher *et al.* 1943). An estimate of α can be made for any pair of S and N using Newton's method (Condit *et al.* in press). Simpson's index is given by

$$\sum_i f_i^2 \tag{2}$$

where f_i is the relative abundance of species i (Simpson 1949; Kempton 1979). The Shannon–Wiener index is

$$\sum_i -(f_i \ln f_i) \tag{3}$$

(Pielou 1966, 1975; Kempton 1979). The dominance index is the largest f_i, or the relative abundance of the most numerous species in a quadrat (Berger & Parker 1970). All indices were calculated for each individual quadrat.

In addition, we tested two more recently developed 'nonparametric' indices, the Chao and the second-order jackknife estimators of species richness (Heltsche & Forrester 1983; Chao 1984; Colwell & Coddington 1994). In contrast to the four indices listed above, these are not arbitrary metrics of diversity but are supposed to yield estimates of total species richness. The Chao index C is given by

$$C = S + \left(\frac{S_1^2}{2S_2} \right) \tag{4}$$

and the jackknife index J by

$$J = S + \left\{ \frac{S_1(2N-3)}{N} - \frac{S_2(N-2)^2}{N(N-1)} \right\} \tag{5}$$

where S_1 is the total number of species represented by a single individual, S_2 by two individuals, and S and N as defined above. (S_1 and S_2 can alternatively represent the number of species found in one subsample and two subsamples, respectively, of a larger sample. We tested this alternative by defining subsamples as 5-m × 5-m, 10-m × 10-m or 20-m × 20-m subquadrats of larger quadrats and found estimates nearly identical to those given by eqns 4 and 5; we report on just the latter.)

EXPECTED NUMBER OF SPECIES

We also make use of a formulation for the 'expected' number of species in a subsample of individuals drawn from a larger known sample; in our study, the larger sample was the entire 50-ha plot. This is equivalent to randomizing the order in which individuals are added in a species–individual curve. Given a set of abundances N_i for S species, and $N = \Sigma_i N_i$, the number of species s in a subsample of n plants taken at random from the larger sample is

$$s = \sum_i p_i(N_i, N, n) \tag{6}$$

where $p_i(N_i, N, n)$ is the probability of encountering species i in the subsample (Hurlbert 1971). This probability is found from a hypergeometric formulation,

$$p_i(N_i, N, n) = 1 - \left[\left(\frac{N-N_i}{N} \right) \right.$$
$$\left. \left(\frac{N-N_i-1}{N-1} \right) \left(\frac{N-N_i-2}{N-2} \right) \cdots \left(\frac{N-N_i-n+1}{N-n+1} \right) \right\}. \tag{7}$$

Hubbell & Foster (1983, 1992) made analogous calculations for the number of species expected in small areas within the BCI 50-ha plot. This *s* illustrates the impact of contagion on the species–accumulation curve, since *s* will equal *S* from a subregion only if species are randomly intermingled (Hubbell & Foster 1992).

SPECIES PER FIXED INDIVIDUAL COUNT

To compare species richness and estimators of diversity between d.b.h. classes or between plots, we needed estimates from precisely the same numbers of individuals. We generated these by simple linear interpolation on semilog plots, i.e., richness or diversity indices vs. the logarithm of the number of individuals. For example, to calculate species richness in exactly 500 individuals $\geq$ 10 mm d.b.h. at BCI, we plotted mean species number vs. the logarithm of mean individual number for all quadrat sizes from 5-m $\times$ 5-m to 500-m $\times$ 500-m, connected the points with lines, and then read off the value at 500 plants. Semilog plots were most appropriate because they were either straight lines or slowly bending curves across a wide range of individuals for all indices.

Results

SPECIES–AREA CURVES

The form of the species–area curve from all three forests was similar. On semilog plots, curves were nearly linear for stems $\geq$ 10 mm d.b.h., but concave upward for larger d.b.h. classes. On log–log plots (Fig. 1), species–area curves were concave downward, but curves from different d.b.h. classes were not parallel. They converged as area increased, reflecting an increase in the proportion of total species that fell in the larger d.b.h. classes with increasing area. For example, at BCI, in 20-m $\times$ 20-m quadrats (0.04 ha), less than a quarter of the species were $\geq$ 100 mm (12 species $\geq$ 100 mm d.b.h. and 54 species $\geq$ 10 mm), compared with nearly 60% (163 of 280) in 25 ha quadrats. The pattern was similar at Pasoh (Fig. 1). At Mudumalai, the curves also converged, but not nearly as much: even in the smallest quadrats, most species were $\geq$ 100 mm d.b.h. Tables 1–3 give full datasets on species number in different areas and different d.b.h. classes in all three plots.

SPECIES–INDIVIDUAL CURVES

In contrast, when species number was plotted against the number of individuals, different d.b.h. classes fell on nearly identical curves. That is, in all three forests, the number of species in a given number of individuals was nearly independent of d.b.h. class. On semilog plots, species–individual curves were concave upward for < 500 stems, then became linear; at Pasoh and
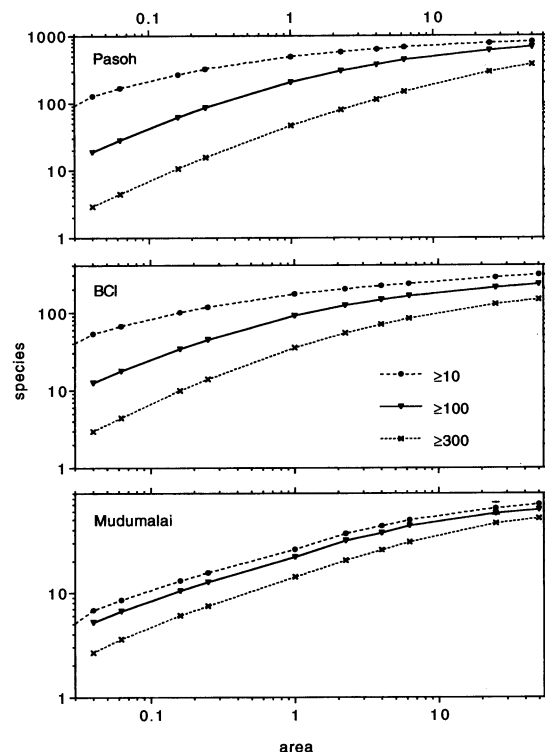

Fig. 1 Species–area curves from three 50-ha plots, three different d.b.h. classes at each, plotted on log–log scales. Vertical bars show 95% confidence limits for species number; when not visible, confidence limits were too small to show up on the graph. All points are from square quadrats except the right-most, which are from the entire 1000 m $\times$ 500 m (the latter do not have confidence limits).

Mudumalai, they became slightly concave downward in the largest samples (Fig. 2). On log–log plots, the curves were concave downward (Fig. 3), with essentially the same form in all three forests.

The slope of the log–log species–individual curves (the '*z*-value') declined with individual number in all three plots, reaching a value of around 0.10 in the largest samples (Fig. 4). At Pasoh, the slope from 50 ha to the entire Malay Peninsula was 0.11. In Panama, *z* was 0.13 from 50 ha to 1500 ha (all Barro Colorado Island) and from there to the entire Canal Area (Fig. 4), while it was 0.29 from the Canal Area to the rest of Panama. In India, *z* = 0.17 from 50 ha to the 32 000 ha in Mudumalai (Fig. 4).

DIVERSITY DIFFERENCES BETWEEN FORESTS

In samples > 3000 individuals, the Pasoh forest consistently had 2.7 times as many species as BCI (Fig. 5). In smaller samples, the difference was less, and in samples of < 10 individuals, the forests were barely different. Comparing BCI and Mudumalai, the difference in species richness reached a plateau at about 300 individuals, with Mudumalai 0.3 times as rich as BCI. To compare Pasoh and Mudumalai, one would divide the value from the top curve by the value from the bottom in Fig. 5; this would reach an

Table 1 Means and 95% confidence intervals for species number in the Pasoh 50-ha plot (confidence limits were calculated with a *t*-statistic). The largest quadrat, 1000 m × 500 m, is the entire plot, so there were no replicates and thus no confidence limits. The mean number of stems for any quadrat size can be calculated from the mean density per ha over the whole plot: 6702.0 for stems ≥ 10 mm d.b.h., 3879.1 for stems ≥ 20 mm, 2566.2 for stems ≥ 25.4 mm, 2123.8 for stems ≥ 31.8 mm, 1371.6 for stems ≥ 50 mm, 529.0 for stems ≥ 100 mm, 168.1 for stems ≥ 200 mm, 75.4 for stems ≥ 300 mm, 40.3 for stems ≥ 400 mm, and 14.3 for stems ≥ 600 mm. The actual number of stems for 40-m × 40-m and 150-m × 150-m plots were slightly different, because these quadrat dimensions did not cover the entire 50 ha

Quadrat size (m)	Size class (mm d.b.h.)									
	≥ 10	≥ 20	≥ 25.4	≥ 31.8	≥ 50	≥ 100	≥ 200	≥ 300	≥ 400	≥ 600
20 × 20	126.8±0.8	91.8±0.6	69.8±0.5	60.9±0.4	43.2±0.3	18.8±0.2	6.3±0.1	2.9±0.1	1.6±0.1	0.6±0.0
25 × 25	166.9±1.1	124.4±0.9	96.9±0.7	85.5±0.6	62.0±0.5	28.0±0.3	9.6±0.2	4.4±0.1	2.4±0.1	0.9±0.1
40 × 40	267.3±2.0	213.1±1.6	175.5±1.4	159.1±1.4	122.9±1.2	61.0±0.8	22.5±0.5	10.6±0.3	5.8±0.3	2.1±0.2
50 × 50	323.0±2.7	265.1±2.3	223.5±2.1	205.1±2.0	163.3±1.7	85.5±1.3	32.7±0.8	15.6±0.5	8.6±0.4	3.2±0.2
100 × 100	494.5±6.2	438.1±6.2	395.3±6.0	375.6±6.0	326.8±5.7	205.9±4.8	92.1±3.7	46.3±2.3	26.2±1.6	9.9±0.8
150 × 150	581.4±10.8	531.2±12.9	493.6±12.4	475.9±12.6	429.9±12.1	303.9±12.9	151.1±9.9	79.6±7.3	45.6±4.5	17.9±2.6
200 × 200	634.6±12.3	588.5±16.7	551.8±18.6	536.1±18.9	498.4±16.9	374.0±16.7	204.3±15.2	113.2±11.4	65.9±7.1	26.3±3.6
250 × 250	681.4±15.9	638.8±23.0	606.9±26.2	592.0±27.0	557.5±22.3	441.4±23.2	260.3±23.6	147.9±18.5	85.8±10.6	34.3±6.6
500 × 500	782.0±3.9	754.0±0.0	732.0±17.3	722.5±15.2	694.5±10.8	607.5±2.9	441.5±8.8	293.0±34.6	181.5±28.4	75.5±23.8
1000 × 1	256.4±1.1	194.1±1.0	153.2±0.9	136.0±0.8	99.6±0.8	45.4±0.6	15.6±0.3	7.1±0.2	3.9±0.2	1.4±0.1
500 × 2	245.1±1.3	186.4±1.1	147.7±0.9	131.4±0.9	97.0±0.8	44.6±0.6	15.4±0.3	7.1±0.2	3.8±0.2	1.4±0.1
200 × 2	139.6±0.7	99.4±0.5	74.7±0.4	64.8±0.4	45.4±0.3	19.4±0.2	6.4±0.1	2.9±0.1	1.6±0.1	0.6±0.0
400 × 4	297.0±2.1	234.4±1.7	192.2±1.4	173.6±1.3	132.6±1.2	64.8±0.9	23.2±0.6	10.8±0.4	5.9±0.3	2.1±0.2
500 × 5	357.9±2.6	292.8±2.3	246.4±2.1	225.6±1.9	178.1±1.6	92.0±1.2	34.4±0.8	16.2±0.5	8.9±0.4	3.4±0.3
1000 × 10	544.5±5.3	484.0±5.2	438.5±5.1	416.2±5.2	361.6±5.1	226.9±4.3	100.6±3.2	50.1±1.8	28.3±1.2	11.0±0.9
500 × 20	520.9±6.0	464.0±6.6	420.0±6.2	398.3±6.1	346.2±5.6	218.2±4.6	97.3±3.2	48.3±2.1	27.0±1.5	10.5±1.0
1000 × 500	817	799	781	773	752	683	525	377	248	102

Table 2 Means and 95% confidence intervals for species number in the Barro Colorado Island 50-ha plot (confidence limits were calculated with a *t*-statistic). The largest quadrat, 1000 × 500 m, is the entire plot, so there were no replicates and thus no confidence limits. The mean number of stems for any quadrat size can be calculated from the mean density per ha over the whole plot: 4881.8 for stems ≥ 10 mm d.b.h., 2885.6 for stems ≥ 20 mm, 2201.1 for stems ≥ 25.4 mm, 1740.4 for stems ≥ 31.8 mm, 1022.4 for stems ≥ 50 mm, 424.8 for stems ≥ 100 mm, 155.1 for stems ≥ 200 mm, 82.4 for stems ≥ 300 mm, 47.2 for stems ≥ 400 mm, and 17.3 for stems ≥ 600 mm. The actual number of stems for 40-m × 40-m and 150-m × 150-m plots were slightly different, because these quadrat dimensions did not cover the entire 50 ha

Quadrat size (m)	Size class (mm d.b.h.)									
	≥ 10	≥ 20	≥ 25.4	≥ 31.8	≥ 50	≥ 100	≥ 200	≥ 300	≥ 400	≥ 600
20 × 20	53.7±0.5	42.6±0.4	37.4±0.4	33.1±0.4	23.7±0.3	12.5±0.2	5.3±0.1	3.0±0.1	1.8±0.1	0.7±0.0
25 × 25	67.4±0.7	54.9±0.6	49.0±0.6	43.8±0.5	32.3±0.4	17.7±0.3	7.7±0.2	4.4±0.1	2.7±0.1	1.0±0.1
40 × 40	100.6±1.2	86.6±1.1	79.6±1.1	73.3±1.1	57.5±1.0	34.1±0.6	16.4±0.4	9.9±0.3	6.2±0.2	2.5±0.2
50 × 50	117.8±1.4	104.1±1.4	96.9±1.3	90.3±1.3	72.9±1.2	44.9±0.8	22.7±0.5	13.8±0.4	8.8±0.4	3.7±0.2
100 × 100	172.4±2.4	160.2±2.4	153.0±2.3	147.3±2.2	128.7±2.4	91.2±1.9	53.6±1.2	35.2±1.4	24.1±1.1	11.2±0.9
150 × 150	200.6±3.9	190.7±3.8	184.2±3.8	178.4±3.9	162.6±3.4	123.5±3.6	78.0±2.5	54.4±2.5	38.2±2.0	20.2±2.3
200 × 200	219.3±5.9	208.9±5.7	203.9±6.1	199.4±5.7	184.0±4.9	145.8±5.2	99.2±4.9	70.0±4.0	51.2±3.0	28.7±3.3
250 × 250	232.9±6.5	222.6±6.1	217.8±7.2	213.4±7.3	200.6±7.0	162.8±5.6	116.0±6.1	83.8±5.2	61.1±4.8	35.6±5.4
500 × 500	279.5±2.9	265.5±10.8	261.5±15.2	259.5±19.5	242.5±1.0	208.0±3.9	163.0±2.0	127.5±6.5	95.5±1.0	59.5±10.8
1000 × 1	98.3±0.6	82.3±0.6	74.0±0.6	66.8±0.5	50.0±0.5	28.1±0.4	12.4±0.3	7.1±0.2	4.3±0.2	1.7±0.1
500 × 2	94.3±0.6	78.8±0.6	71.0±0.6	64.1±0.6	48.5±0.5	27.4±0.4	12.2±0.3	7.1±0.2	4.3±0.2	1.7±0.1
200 × 2	58.8±0.4	46.3±0.4	40.4±0.3	35.4±0.3	25.1±0.3	13.2±0.2	5.5±0.1	3.1±0.1	1.8±0.1	0.7±0.0
400 × 4	109.2±1.1	94.3±1.0	86.7±1.0	79.8±0.9	62.7±0.9	36.8±0.6	17.2±0.4	10.2±0.3	6.3±0.3	2.5±0.2
500 × 5	129.5±1.1	114.3±1.1	106.2±1.0	98.9±1.0	80.0±1.0	49.2±0.7	24.3±0.5	14.8±0.4	9.6±0.4	3.9±0.2
1000 × 10	189.0±2.0	175.4±1.9	168.2±1.8	161.6±1.6	142.4±1.7	100.2±1.6	58.4±1.2	38.9±1.1	26.5±0.9	12.7±0.8
500 × 20	180.8±2.3	168.3±2.1	161.4±2.1	155.1±2.2	136.1±2.3	96.0±1.7	55.9±1.3	37.3±1.1	25.5±1.0	12.0±0.7
1000 × 500	303	291	287	284	269	229	181	146	112	69

asymptote at about 10^4 stems, with Pasoh 9.0 times richer than Mudumalai.

SPECIES–INDIVIDUAL CURVES FOR DIFFERENT D.B.H. CLASSES

Species–accumulation curves from nonoverlapping (and thus independent) d.b.h. classes were identical in form to those in Figs 1–3, and are not shown. Instead, we focus on the number of species in a fixed number of individuals in each d.b.h. class (Fig. 6). For BCI and Pasoh, richness peaked at d.b.h. 50–150 mm. At

Mudumalai, though, the curves were essentially flat across all values of d.b.h.

SPECIES–INDIVIDUAL CURVES FOR CONSTANT AREA

Within square quadrats of 20, 25, 40 and 50 m on a side, species number correlated strongly with individual number in all three forests ($P < 0.01$ for regressions of species number vs. the logarithm of individual number, all four quadrat sizes in all three plots). The slope of the species–individual curve

Table 3 Means and 95% confidence intervals for species number in the Mudumalai 50-ha plot (confidence limits were calculated with a t-statistic). The largest quadrat, 1000×500 m, is the entire plot, so there were no replicates and thus no confidence limits. The mean number of stems for any quadrat size can be calculated from the mean density per ha over the whole plot: 513.8 for stems $\geqslant 10$ mm d.b.h., 472.1 for stems $\geqslant 20$ mm, 451.4 for stems $\geqslant 25.4$ mm, 443.0 for stems $\geqslant 31.8$ mm, 412.3 for stems $\geqslant 50$ mm, 300.8 for stems $\geqslant 100$ mm, 177.4 for stems $\geqslant 200$ mm, 97.6 for stems $\geqslant 300$ mm, 53.7 for stems $\geqslant 400$ mm, and 11.2 for stems $\geqslant 600$ mm. The actual number of stems for 40-m $\times$ 40-m and 150-m $\times$ 150-m plots were slightly different, because these quadrat dimensions did not cover the entire 50 ha

| Quadrat size (m)	Size class (mm d.b.h.)									
	$\geqslant 10$	$\geqslant 20$	$\geqslant 25.4$	$\geqslant 31.8$	$\geqslant 50$	$\geqslant 100$	$\geqslant 200$	$\geqslant 300$	$\geqslant 400$	$\geqslant 600$
20×20	6.8 ± 0.1	6.4 ± 0.1	6.2 ± 0.1	6.1 ± 0.1	5.9 ± 0.1	5.2 ± 0.1	4.0 ± 0.1	2.7 ± 0.1	1.7 ± 0.1	0.4 ± 0.0
25×25	8.6 ± 0.2	8.1 ± 0.2	7.8 ± 0.2	7.8 ± 0.2	7.5 ± 0.2	6.7 ± 0.1	5.2 ± 0.1	3.6 ± 0.1	2.3 ± 0.1	0.6 ± 0.1
40×40	13.1 ± 0.3	12.5 ± 0.3	12.2 ± 0.3	12.1 ± 0.3	11.8 ± 0.3	10.5 ± 0.3	8.4 ± 0.2	6.1 ± 0.2	4.1 ± 0.2	1.4 ± 0.1
50×50	15.6 ± 0.5	15.0 ± 0.4	14.6 ± 0.4	14.5 ± 0.4	14.1 ± 0.4	12.7 ± 0.4	10.3 ± 0.3	7.5 ± 0.3	5.2 ± 0.3	1.9 ± 0.2
100×100	26.2 ± 1.3	25.3 ± 1.2	24.8 ± 1.1	24.6 ± 1.1	24.1 ± 1.0	22.1 ± 0.8	18.3 ± 0.6	14.3 ± 0.7	10.0 ± 0.8	4.6 ± 0.7
150×150	37.1 ± 2.1	35.7 ± 1.9	35.0 ± 1.8	34.8 ± 1.8	34.0 ± 1.6	31.7 ± 1.4	25.8 ± 1.2	20.6 ± 1.3	14.8 ± 1.3	7.6 ± 1.2
200×200	43.9 ± 3.9	42.4 ± 4.1	41.3 ± 3.7	41.0 ± 3.7	40.4 ± 2.8	37.6 ± 2.3	31.2 ± 1.1	25.8 ± 2.1	18.7 ± 2.1	9.9 ± 1.8
250×250	49.9 ± 3.3	47.9 ± 3.8	47.0 ± 3.7	46.8 ± 3.8	46.0 ± 2.7	44.1 ± 1.9	36.6 ± 1.5	30.8 ± 1.6	23.5 ± 2.0	12.4 ± 1.6
500×500	65.0 ± 3.9	63.5 ± 10.8	62.0 ± 13.0	61.0 ± 17.3	60.5 ± 6.9	58.0 ± 2.0	53.5 ± 2.9	46.5 ± 2.2	40.0 ± 0.0	19.5 ± 2.2
1000×1	13.7 ± 0.2	13.0 ± 0.2	12.6 ± 0.2	12.5 ± 0.2	12.1 ± 0.2	10.4 ± 0.2	7.8 ± 0.2	5.3 ± 0.1	3.3 ± 0.1	1.0 ± 0.1
500×2	13.1 ± 0.2	12.5 ± 0.2	12.1 ± 0.2	12.0 ± 0.2	11.6 ± 0.2	10.1 ± 0.2	7.6 ± 0.2	5.2 ± 0.2	3.3 ± 0.1	1.0 ± 0.1
200×2	7.9 ± 0.1	7.4 ± 0.1	7.2 ± 0.1	7.1 ± 0.1	6.8 ± 0.1	5.8 ± 0.1	4.3 ± 0.1	2.8 ± 0.1	1.7 ± 0.1	0.4 ± 0.0
400×4	15.8 ± 0.3	15.0 ± 0.3	14.6 ± 0.3	14.4 ± 0.3	14.0 ± 0.3	12.2 ± 0.3	9.3 ± 0.2	6.5 ± 0.2	4.4 ± 0.2	1.5 ± 0.1
500×5	18.6 ± 0.4	17.8 ± 0.4	17.4 ± 0.3	17.2 ± 0.3	16.8 ± 0.3	14.8 ± 0.3	11.6 ± 0.3	8.4 ± 0.3	5.6 ± 0.2	2.1 ± 0.2
1000×10	31.6 ± 0.9	30.1 ± 0.9	29.5 ± 0.9	29.2 ± 0.8	28.7 ± 0.8	26.0 ± 0.8	21.5 ± 0.7	16.5 ± 0.8	11.5 ± 0.7	5.3 ± 0.5
500×20	29.6 ± 1.0	28.4 ± 1.0	27.8 ± 0.9	27.6 ± 0.8	27.0 ± 0.8	24.6 ± 0.7	20.3 ± 0.7	15.7 ± 0.7	11.2 ± 0.7	5.2 ± 0.5
1000×500	71	69	67	67	66	63	59	52	45	25
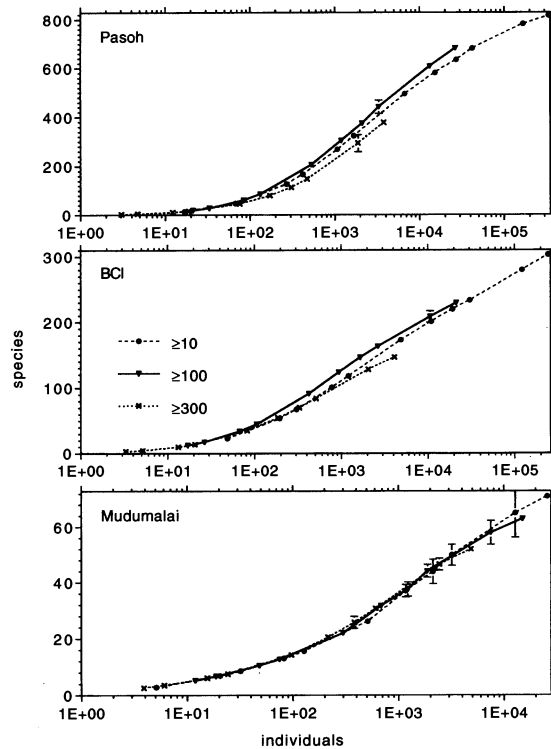
Fig. 2 Species–individual curves from three 50-ha plots, three different d.b.h. classes at each, plotted on semilog scales (the horizontal axis is logarithmic; $1E + 02$ means 10^2, etc.). Vertical bars show 95% confidence limits for species number; when not visible, confidence limits were too small to show up on the graph. All points are from square quadrats except the right-most, which are from the entire 1000 m $\times$ 500 m (the latter do not have confidence limits).
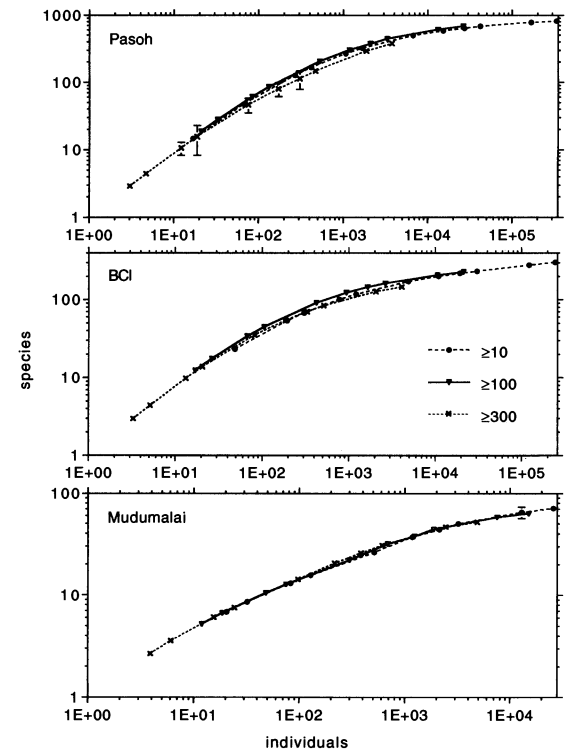

Fig. 3 Species–individual curves from three 50-ha plots, three different d.b.h. classes at each, plotted on log–log scales. Vertical bars show 95% confidence limits for species number; confidence limits for the numbers of individuals are not shown. All points are from square quadrats except the right-most, which are from the entire 1000 m $\times$ 500 m (the latter do not have confidence limits).
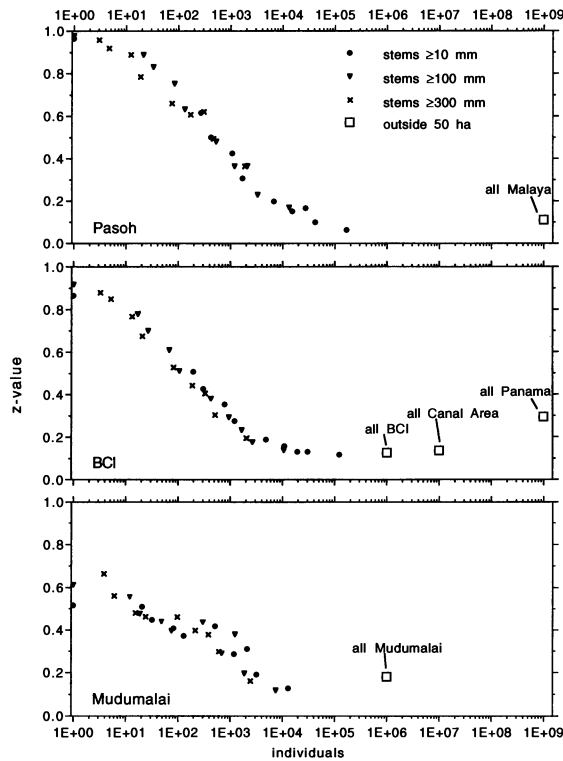
Fig. 4 Slope of log–log species–individual curves (z-values) for three 50-ha plots and from 50-ha plots to larger regions. Slopes were calculated separately for each d.b.h. class, $z_i = (\log S_{i+1} - \log S_i)/(\log N_{i+1} - \log N_i)$, where S_i and N_i are mean species number and mean individual number for one particular quadrat size, and $i + 1$ means the quadrat size next larger than i. Each z_i was plotted against N_i, except that the last two estimates of z were plotted at $N = 10^6$ for all BCI and all Mudumalai, $N = 10^7$ for the Panama Canal area, and $N = 10^9$ for all Panama and all Malaysia.

Fig. 6 Number of species in square plots having exactly 500 individuals (above) or 3000 individuals (below), plotted as a function of d.b.h. class for three different forests. Observed numbers of species (found by interpolation, as described in the Methods section) are plotted as solid lines. Dashed lines give the expected number of species, taken from eqn 6 in the text. The species scale is logarithmic; on the bottom panel it runs from 100 to 500 in units of 100. D.b.h. classes are 'closed', that is bounded at the smaller and the larger d.b.h.; d.b.h. ranges are given in the methods section. Vertical lines show 95% confidence limits. There is no curve for Mudumalai in the bottom figure because most d.b.h. classes did not have 3000 individuals in 50 ha.

within a quadrat of a given area was usually quite similar to that calculated between quadrats of different areas, however, when they differed, they always did so in the same way: quadrats of a smaller area tended to have fewer species than quadrats of a larger area with the same number of individuals. Thus area
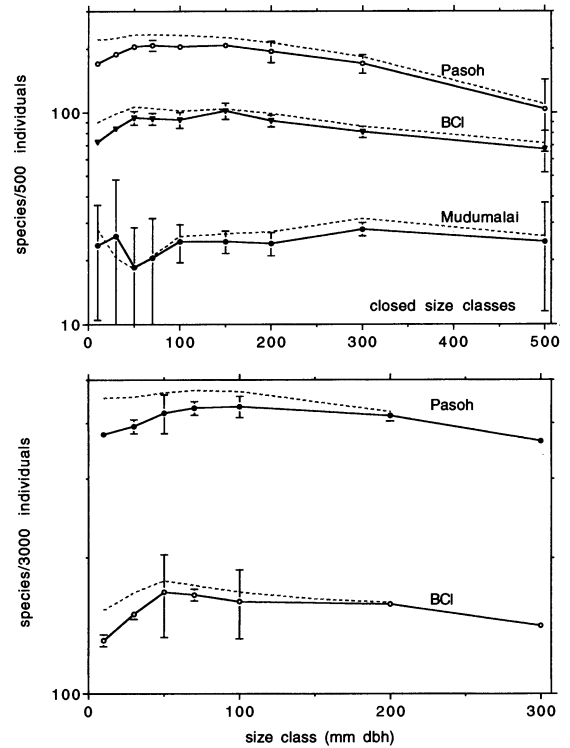
did have an effect, but the differences were slight and sometimes nonexistent: in many cases, quadrats of the larger area did not have more species. In squares 100 m on a side, there was no relationship between
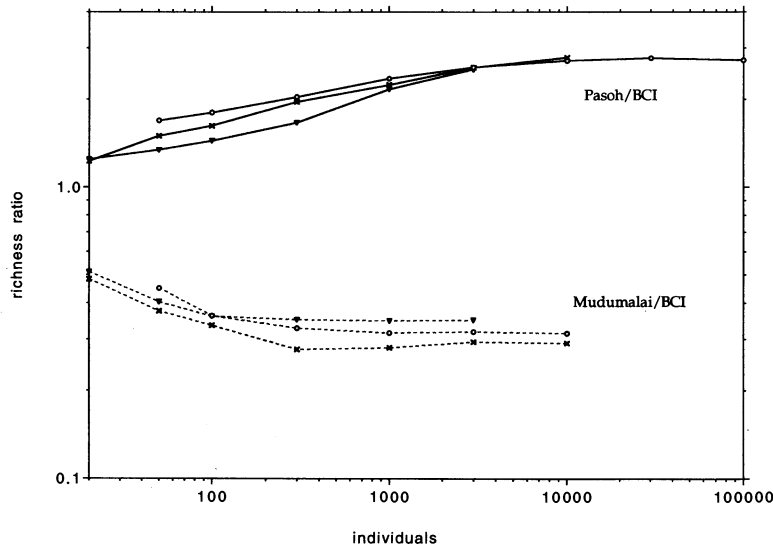

Fig. 5 The ratio of species number found at Pasoh (or Mudumalai) to the species number found at BCI for a given number of individuals, plotted against the number of individuals on a log scale. Interpolation was used as described in the methods. Open circles: stems $\geqslant 10$ mm d.b.h.; crosses: stems $\geqslant 100$ mm d.b.h.; triangles: stems $\geqslant 300$ mm d.b.h. No confidence limits are shown.

species number and individual number. This may just be due to the narrow range of variation in the number of individuals in large quadrats.

RECTANGULAR QUADRATS

Rectangular quadrats had more species than square quadrats of the same area. For rectangles with dimensions 100 times wider than long, there were about 10% more species than in squares of the same area at BCI and Pasoh, but 20% more at Mudumalai (Fig. 7, Table 4). This was true for all d.b.h. classes in samples of > 40 individuals (Fig. 7). Wider rectangles (500 m × 20 m) were intermediate in species number, being 5% more diverse than squares at BCI and Pasoh and 10% more diverse at Mudumalai (Fig. 7, Table 4). Very narrow rectangles, 1000 m × 1 m, were even more diverse, 18% more so than squares at BCI, 19% at Pasoh, and 27% at Mudumalai (Table 4).

EXPECTED SPECIES RICHNESS

At all three plots, there were fewer species in square quadrats compared to random collections from
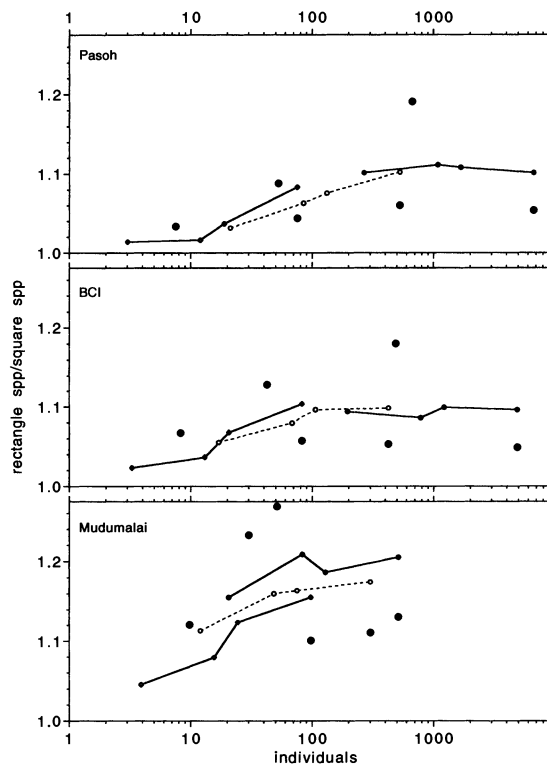

Fig. 7 Ratio of species number in a rectangle to species number in a square of the same area, plotted against the number of individuals on a log scale, for three different forests. The lines connect points from four quadrat sizes of the same shape (200 m × 2 m, 400 m × 4 m, 500 m × 5 m and 1000 m × 10 m); the left-most line is for stems ≥ 300 mm d.b.h., the dotted line for stems ≥ 100 mm, and the right-most line for stems ≥ 10 mm d.b.h. The three large circles above the lines show the ratio for 1000-m × 1-m quadrats, the three circles below for 500-m × 20-m quadrats. In each case, there is one point for stems ≥ 10, one for stems ≥ 100, and one for stems ≥ 300 mm d.b.h. No confidence limits are shown.

throughout the 50 ha (as calculated by Hurlbert's formula for expected species number). The difference was greatest in the smallest d.b.h. classes at Pasoh and BCI, but in the largest d.b.h. classes at Mudumalai (Fig. 6). Rectangular quadrats had species richness approaching the expected value, but always slightly below (Table 4); the narrowest rectangles (1000 m × 1 m) almost matched the expected species count.

DIVERSITY INDICES

All diversity indices, including the nonparametric estimators, increased with the number of individuals in a sample, and in all but Fisher's α, the increase was monotonic. Fisher's α increased with sample size in small samples, then declined, peaking at 2000–12 000 stems in all three plots (varying with d.b.h. class). All indices showed rapid increases in small samples (< 500 individuals), then increased much more slowly.

The degree of dependence on sample size varied between indices. The jackknife estimator was the most variable: it increased by more than 2.5-fold between samples of 10^2 and 10^4 individuals within a d.b.h. class (2.5–4.4 fold increase in different plots and different d.b.h. classes, not including the class ≥ 300 mm d.b.h., which never included 10^4 individuals). Next most variable were the Chao index, which increased by 2.5–3.6-fold over the same range, the Simpson's index (1.5–3.3-fold increase), and the dominance index (1.2–2.3-fold). Least variable were Fisher's α, with a 1.2–1.9-fold increase, and the Shannon–Wiener, which increased by 1.3–1.6-fold. All were less variable than species richness, which increased by 4.1–8.2-fold within a d.b.h. class over the same range of individuals.

We also calculated the ratio of diversity indices between different plots as a function of the number of individuals sampled, for each d.b.h. class. Fisher's α and the Shannon–Wiener index gave fairly constant estimates of diversity ratios in all samples > 50 individuals. Ratios for Fisher's α were 3.5:1 for Pasoh:BCI and 0.2:1 for BCI:Mudumalai, which are similar to, but somewhat more extreme, than the limiting ratios for species richness shown in Fig. 5. Ratios for the Shannon–Wiener index itself were much lower, but the exponential of the index (e raised to the index) gave diversity ratios very close to those from Fisher's α. Ratios from the dominance and diversity indices were more variable than those for species richness, and those for the Chao and jackknife indices were equally variable. Condit *et al.* (in press) explore the diversity indices in greater detail.

The nonparametric diversity estimators did not serve as predictors of total species richness. Applied to small square quadrats, they always greatly underestimated total species in 50 ha. For example, the jackknife estimator applied to 1 ha quadrats at Pasoh

Table 4 Observed and expected species number for some quadrat sizes and d.b.h. classes, for (A) the Pasoh 50-ha plot, (B) the BCI plot, and (C) the Mudumalai plot. D.b.h. refers to the size range of stems included. Expected number of species was calculated from eqn 6 in the text. For square quadrats, the observed number of species matches that from Tables 1–3. Wider rectangles were 500 m × 2 m for 0.1 ha quadrats and 500 m × 20 m for 1 ha. Narrower rectangles were 100 times wider than long for all quadrats but 0.1 ha, for which they were 1000 m × 1 m. Blanks indicate that richness in rectangles of the given area was not calculated

Quadrat area	d.b.h. (mm)	No. of stems	Expected species	Observed species		
				square	wider rect.	narrower rect.
Pasoh						
0.04 ha	⩾ 10	268.1	159.4	126.8	—	139.6
	⩾ 100	21.2	19.8	18.8	—	19.4
0.1 ha	⩾ 10	670.2	271.6	215.3	245.1	256.4
	⩾ 100	52.9	46.1	41.7	44.6	45.4
0.25 ha	⩾ 10	1675.5	401.8	323.0	—	357.9
	⩾ 100	132.3	97.7	85.5	—	92.0
1.0 ha	⩾ 10	6702.0	579.9	494.5	520.9	544.5
	⩾ 100	529.0	239.0	205.9	218.2	226.9
4.0 ha	⩾ 10	27248.7	706.0	634.6	—	—
	⩾ 100	2101.1	425.1	374.0	—	—
BCI						
0.04 ha	⩾ 10	195.3	67.2	53.7	—	58.8
	⩾ 100	17.0	14.2	12.5	—	13.2
0.1 ha	⩾ 10	488.2	103.4	83.3	94.3	98.3
	⩾ 100	42.5	28.9	24.9	27.4	28.1
0.25 ha	⩾ 10	1220.5	142.6	117.8	—	129.5
	⩾ 100	106.2	52.5	44.9	—	49.2
1.0 ha	⩾ 10	4881.8	199.8	172.4	180.8	189.0
	⩾ 100	424.8	103.7	91.2	96.0	100.2
4.0 ha	⩾ 10	19261.7	244.0	219.3	—	—
	⩾ 100	1657.5	159.9	145.8	—	—
Mudumalai						
0.04 ha	⩾ 10	20.6	9.8	6.8	—	7.9
	⩾ 100	12.0	7.0	5.2	—	5.8
0.1 ha	⩾ 10	51.4	14.2	10.8	13.1	13.7
	⩾ 100	30.1	10.9	8.5	10.1	10.4
0.25 ha	⩾ 10	128.5	20.5	15.6	—	18.6
	⩾ 100	75.2	16.2	12.7	—	14.8
1.0 ha	⩾ 10	513.8	34.7	26.2	29.6	31.6
	⩾ 100	300.8	27.6	22.1	24.6	26.0
4.0 ha	⩾ 10	2127.2	52.1	43.9	—	—
	⩾ 100	1232.9	43.0	37.6	—	—

(stems ⩾ 10 mm d.b.h.) yielded 631 species (mean of 50 quadrats); the total species count for 50 ha was 816, and for 1 ha, 495. The degree of underestimate was essentially identical at BCI and Mudumalai (1 ha of stems ⩾ 10 mm d.b.h.: at BCI, 219 predicted by the jackknife compared to 303 species in 50 ha; at Mudumalai, 38 from the jackknife compared to 71 total). Estimates from smaller quadrats were much lower. Even estimators derived from long, narrow rectangles greatly underestimated true species richness: in 1000-m × 1-m rectangles at Pasoh (stems ⩾ 10 mm d.b.h.), the jackknife estimator was 453 species, less than the actual number observed in square hectares (100 × 100 m) let alone 50 ha. In all examples given above, the Chao estimator was lower than the jackknife.

Discussion

Several novel patterns in species–accumulation curves appeared in these three forests, and they have impli-

cations for community theory and for the practice of measuring species diversity. We were able to detect novel patterns because of the unique dataset – precise enumeration of large numbers of individuals in three tropical forests based on a strictly comparable methodology. Because the three forests are very different – with no species in common, isolated from one another for tens of millions of years – it is tempting to generalize about the patterns that appeared at all three. Further observations, from new sites, will put these generalizations to the test.

A simple yet important pattern is that species continued to accumulate in all three inventories up to and beyond 50 ha. There was no asymptote in the accumulation curves at any scale. This contradicts a widely held belief among tropical ecologists that tree species richness reaches an asymptote at 1–3 ha (Boom 1986; Gentry 1988; Tuomisto *et al*. 1995). The expectation of an asymptote probably comes from temperate forest ecology, where sharply delimited

communities defined by edaphic and climatic regimes can be fully enumerated.

Does the lack of an asymptote suggest that these forests lack well-defined tree communities? Most models of community structure based on habitat partitioning suggest that there will be an asymptote in the species–accumulation curve. On the other hand, the lack of an asymptote is a prediction of a spatially explicit, zero-sum, community drift model that incorporates speciation (Hubbell & Foster 1986; Hubbell 1995, in press). In this model, large numbers of competitively identical species change in abundance due to random drift alone, but short propagule dispersal limits the spatial spread of species. In such a community, there will always be some species with limited ranges and there will always be rare species; rarity and narrow ranges guarantee that a species–accumulation curve will continue to increase at all scales until the boundary of a continent is reached.

The drift theory also has explicit predictions about the form of the species–accumulation curve. Hubbell (in press) demonstrates that a community at drift – without dispersal limitation – will generate a species–accumulation curve much like that predicted by Fisher *et al.* (1943), indeed, with a constant value of Fisher's parameter. [Watterson (1974) briefly mentions a drift model and his results support this conclusion.] This prediction closely matches our results within 50 ha, since α was fairly constant. A constant value for α means linear species–accumulation with the logarithm of individual number, and concomitantly, a diminishing slope on a log–log plot: $z = (\alpha/S)$ if α is constant (z is the log–log slope, S is species number). Since z actually increased at scales much larger than 50 ha, it is evident that the communities are not subject to pure drift at large scales. There are a variety of possible explanations, an obvious one being habitat heterogeneity, which is supported by the contrast between Panama and Malaysia: z increased sharply in Panama, but was near-constant in Malaysia. Indeed, despite a three-fold higher species richness within the 50-ha plots, Malaysia has approximately the same number of tree and shrub species (3197) as Panama (2850), even though Panama is smaller. This fits with the relatively uniform climate and geology of the Malay Peninsula, in contrast to a highly variable environment (rainfall, elevation) in Panama (Kochummen *et al.* 1992; provide an interesting discussion of the distribution of the Malaysian flora). We speculate that Malaysia and the Panama Canal area behave much like single large communities at drift, with only moderate habitat heterogeneity, whereas across all of Panama, sharp habitat boundaries affect many species' ranges. The Mudumalai 50-ha plot is also in the midst of a sharp climatic gradient, and this fits with a z-value rising sharply beyond 50 ha.

No other theory of community structure provides such accurate predictions about z. Preston (1948, 1962) claimed that z should be 0.28, but this was no more than an empirical observation, and May (1975) illustrated that a wide range of species abundance distributions lead to z-values between 0.1 and 0.4. Since the community drift theory predicts changes in z very close to those observed – rapid decreases in small samples, reaching about 0.1 in 50 ha – our observations are remarkable corroboration of the importance of drift in the structure of these communities.

Species–accumulation curves for different d.b.h. classes within each forest were nearly identical. To the degree that they were similar, this suggests that larger d.b.h. classes were essentially random samples of smaller. There were slight differences among d.b.h. classes, though, with slight peaks in species richness at intermediate sizes (50–150 mm) at both Pasoh and BCI (but not at Mudumalai). The decline in richness among larger d.b.h.s is not surprising, since there are species which simply never achieve large sizes. The slight increase in species richness with small d.b.h.s suggests density-dependent effects: first, a spatial effect in which dense family aggregations around parent trees are thinned by pest pressure relative to more dispersed saplings of the same species (Janzen 1970; Connell 1971; Augspurger 1983; Clark & Clark 1984; Hubbell *et al.* 1990; Condit *et al.* 1992a, 1994; Gilbert *et al.* 1994; Condit 1995); and, secondly, an abundance effect, whereby abundant species suffer greater mortality at the sapling stage. The former changes spatial patterns, breaking up species clusters without changing the total abundance distribution; the latter changes the total abundance distribution without having any spatial effect.

The comparison of observed and 'expected' species richness illuminates the relevance of density-dependence. At both BCI and Pasoh, expected species richness increased slightly with d.b.h. at small d.b.h.s, suggesting weak, nonspatial density-dependence. At all d.b.h. classes, observed species richness in square quadrats was less than expected (as already noted for BCI by Hubbell & Foster 1992); rectangular quadrats were intermediate in richness. These observations are consistent with aggregated distributions of individual species at all d.b.h.s, but the fact that observed richness deviated most from expected in the smallest d.b.h. classes suggests that there was weak spatially explicit density-dependence (as we observed with more direct methods at BCI; see Condit *et al.* 1994). At Mudumalai, there was no evidence for density-dependence in species richness patterns.

All of these observations have important implications for diversity inventories of tropical forests. We have written a manual with precise recommendations about tropical tree inventories (Condit *et al.* in press); here we summarize the main conceptual points.

First, since species accumulated simply and predictably as a function of individuals counted, but not as a function of area, species–individual curves are more useful for assessing and comparing diversity than species–area curves. Since different d.b.h. classes

accumulated species at similar rates, studies based on different stem d.b.h.s can be compared simply by evaluating the same number of individuals. Previous studies have recognized that species–accumulation can be predicted better by counting individuals rather than area (Ashton 1977; Angermeier & Schlosser 1989), but we know of no other evaluation of species accumulation in different size or age classes within a community.

Secondly, since very small samples showed little difference in species richness, richness alone should not be used as a diversity indicator when fewer than 1000 stems are sampled. Fortunately, two indices of diversity worked fairly well in capturing diversity ratios in small samples: Fisher's α and the exponential of the Shannon–Wiener index. Differences indicated by these diversity indices matched the asymptotic ratios of species richness found in large samples. Other indices were not useful in this regard, and particularly disappointing were the 'nonparametric' indices, much discussed recently and even applied to tropical forest data (Colwell & Coddington 1994).

Condit *et al.* (in press) also discuss in detail methods for extrapolating species richness to larger areas. One approach is to assume a constant value of Fisher's α, which, as indicated above, has theoretical justification in homogeneous communities. This worked quite well within 50 ha at all three sites, suggesting that one can predict richness in 50 ha from samples of only 1000 stems. Beyond 50 ha, though, a constant z-value would be a better predictor than a constant α; indeed, assuming constant z yielded reasonable extrapolations from 50 ha to substantially larger areas where environmental heterogeneity was minimal. When there is major environmental heterogeneity, however, predictions using either α or z can substantially underestimate total richness. New theoretical approaches addressing changes in species composition with environmental changes are needed.

We hope to have illustrated that there remains much to learn about the species–accumulation function that is highly pertinent to important questions in ecology. Our large-scale and intensive inventories of species-rich forests provide data to test oft-debated empirical patterns and are helping to develop a new theoretical understanding of what forces control community structures at many scales.

Acknowledgements

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Table 1. Means and 95% confidence intervals for species number in the Pasoh 50 ha plot (confidence limits were calculated with a t-statistic). The largest quadrat, 1000 x 500 m, is the entire plot, so there were no replicates and thus no confidence limits. The mean number of stems for any quadrat size can be calculated from the mean density per ha over the whole plot: 6702.0 for stems >= 10 mm dbh, 3879.1 for stems >= 20 mm, 2566.2 for stems >= 25.4 mm, 2123.8 for stems >= 31.8 mm, 1371.6 for stems >= 50 mm, 529.0 for stems >= 100 mm, 168.1 for stems >= 200 mm, 75.4 for stems >= 300 mm, 40.3 for stems >= 400 mm, and 14.3 for stems >= 600 mm. The actual number of stems for 40 x 40 m and 150 x 150 m plots were slightly different, because these quadrat dimensions did not cover the entire 50 ha.

Quadrat size (m)	Size class (mm dbh)									
	>= 10	>= 20	>= 25.4	>= 31.8	>= 50	>= 100	>= 200	>= 300	>= 400	>= 600
20x20	126.8±0.8	91.8±0.6	69.8±0.5	60.9±0.4	43.2±0.3	18.8±0.2	6.3±0.1	2.9±0.1	1.6±0.1	0.6±0.0
25x25	166.9±1.1	124.4±0.9	96.9±0.7	85.5±0.6	62.0±0.5	28.0±0.3	9.6±0.2	4.4±0.1	2.4±0.1	0.9±0.1
40x40	267.3±2.0	213.1±1.6	175.5±1.4	159.1±1.4	122.9±1.2	61.0±0.8	22.5±0.5	10.6±0.3	5.8±0.3	2.1±0.2
50x50	323.0±2.7	265.1±2.3	223.5±2.1	205.1±2.0	163.3±1.7	85.5±1.3	32.7±0.8	15.6±0.5	8.6±0.4	3.2±0.2
100x100	494.5±6.2	438.1±6.2	395.3±6.0	375.6±6.0	326.8±5.7	205.9±4.8	92.1±3.7	46.3±2.3	26.2±1.6	9.9±0.8
150x150	581.4±10.8	531.2±12.9	493.6±12.4	475.9±12.6	429.9±12.1	303.9±12.9	151.1±9.9	79.6±7.3	45.6±4.5	17.9±2.6
200x200	634.6±12.3	588.5±16.7	551.8±18.6	536.1±18.9	498.4±16.9	374.0±16.7	204.3±15.2	113.2±11.4	65.9±7.1	26.3±3.6
250x250	681.4±15.9	638.8±23.0	606.9±26.2	592.0±27.0	557.5±22.3	441.4±23.2	260.3±23.6	147.9±18.5	85.8±10.6	34.3±6.6
500x500	782.0±3.9	754.0±0.0	732.0±17.3	722.5±15.2	694.5±10.8	607.5±2.9	441.5±8.8	293.0±34.6	181.5±28.4	75.5±23.8
1000x1	256.4±1.1	194.1±1.0	153.2±0.9	136.0±0.8	99.6±0.8	45.4±0.6	15.6±0.3	7.1±0.2	3.9±0.2	1.4±0.1
500x2	245.1±1.3	186.4±1.1	147.7±0.9	131.4±0.9	97.0±0.8	44.6±0.6	15.4±0.3	7.1±0.2	3.8±0.2	1.4±0.1
200x2	139.6±0.7	99.4±0.5	74.7±0.4	64.8±0.4	45.4±0.3	19.4±0.2	6.4±0.1	2.9±0.1	1.6±0.1	0.6±0.0
400x4	297.0±2.1	234.4±1.7	192.2±1.4	173.6±1.3	132.6±1.2	64.8±0.9	23.2±0.6	10.8±0.4	5.9±0.3	2.1±0.2
500x5	357.9±2.6	292.8±2.3	246.4±2.1	225.6±1.9	178.1±1.6	92.0±1.2	34.4±0.8	16.2±0.5	8.9±0.4	3.4±0.3
1000x10	544.5±5.3	484.0±5.2	438.5±5.1	416.2±5.2	361.6±5.1	226.9±4.3	100.6±3.2	50.1±1.8	28.3±1.2	11.0±0.9
500x20	520.9±6.0	464.0±6.6	420.0±6.2	398.3±6.1	346.2±5.6	218.2±4.6	97.3±3.2	48.3±2.1	27.0±1.5	10.5±1.0
1000x500	817	799	781	773	752	683	525	377	248	102

Table 2. Means and 95% confidence intervals for species number in the Barro Colorado Island 50 ha plot (confidence limits were calculated with a t- statistic). The largest quadrat, 1000 x 500 m, is the entire plot, so there were no replicates and thus no confidence limits. The mean number of stems for any quadrat size can be calculated from the mean density per ha over the whole plot: 4881.8 for stems >= 10 mm dbh, 2885.6 for stems >= 20 mm, 2201.1 for stems >= 25.4 mm, 1740.4 for stems >= 31.8 mm, 1022.4 for stems >= 50 mm, 424.8 for stems >= 100 mm, 155.1 for stems >= 200 mm, 82.4 for stems >= 300 mm, 47.2 for stems >= 400 mm, and 17.3 for stems >= 600 mm. The actual number of stems for 40 x 40 m and 150 x 150 m plots were slightly different, because these quadrat dimensions did not cover the entire 50 ha.

Quadrat size (m)	Size class (mm dbh)									
	>= 10	>= 20	>= 25.4	>= 31.8	>= 50	>= 100	>= 200	>= 300	>= 400	>= 600
20x20	53.7±0.5	42.6±0.4	37.4±0.4	33.1±0.4	23.7±0.3	12.5±0.2	5.3±0.1	3.0±0.1	1.8±0.1	0.7±0.0
25x25	67.4±0.7	54.9±0.6	49.0±0.6	43.8±0.5	32.3±0.4	17.7±0.3	7.7±0.2	4.4±0.1	2.7±0.1	1.0±0.1
40x40	100.6±1.2	86.6±1.1	79.6±1.1	73.3±1.1	57.5±1.0	34.1±0.6	16.4±0.4	9.9±0.3	6.2±0.2	2.5±0.2
50x50	117.8±1.4	104.1±1.4	96.86±1.3	90.3±1.3	72.9±1.2	44.9±0.8	22.7±0.5	13.8±0.4	8.8±0.4	3.7±0.2
100x100	172.4±2.4	160.2±2.4	153.0±2.3	147.3±2.2	128.7±2.4	91.2±1.9	53.6±1.2	35.2±1.4	24.1±1.1	11.2±0.9

150x150	200.6±3.9	190.7±3.8	184.2±3.8	178.4±3.9	162.6±3.4	123.5±3.6	78.0±2.5	54.4±2.5	38.2±2.0	20.2±2.3
200x200	219.3±5.9	208.9±5.7	203.9±6.1	199.4±5.7	184.0±4.9	145.8±5.2	99.2±4.9	70.0±4.0	51.2±3.0	28.7±3.3
250x250	232.9±6.5	222.6±6.1	217.8±7.2	213.4±7.3	200.6±7.0	162.8±5.6	116.0±6.1	83.8±5.2	61.1±4.8	35.6±5.4
500x500	279.5±2.9	265.5±10.8	261.5±15.2	259.5±19.5	242.5±1.0	208.0±3.9	163.0±2.0	127.5±6.5	95.5±1.0	59.5±10.8
1000x1	98.3±0.6	82.3±0.6	74.0±0.6	66.8±0.5	50.0±0.5	28.1±0.4	12.4±0.3	7.1±0.2	4.3±0.2	1.7±0.1
500x2	94.3±0.6	78.8±0.6	70.95±0.6	64.1±0.6	48.5±0.5	27.4±0.4	12.2±0.3	7.1±0.2	4.3±0.2	1.7±0.1
200x2	58.8±0.4	46.3±0.4	40.4±0.3	35.4±0.3	25.1±0.3	13.2±0.2	5.5±0.1	3.1±0.1	1.8±0.1	0.7±0.1
400x4	109.2±1.1	94.3±1.0	86.7±1.0	79.8±0.9	62.7±0.9	36.8±0.6	17.2±0.4	10.2±0.3	6.3±0.3	2.5±0.2
500x5	129.5±1.1	114.3±1.1	106.2±1.0	98.9±1.0	80.0±1.0	49.2±0.7	24.3±0.5	14.8±0.4	9.6±0.4	3.9±0.2
1000x10	189.0±2.0	175.4±1.9	168.2±1.8	161.6±1.6	142.4±1.7	100.2±1.6	58.4±1.2	38.9±1.1	26.5±0.9	12.7±0.8
500x20	180.8±2.3	168.3±2.1	161.4±2.1	155.1±2.2	136.1±2.3	96.0±1.7	55.9±1.3	37.3±1.1	25.5±1.0	12.0±0.7
1000x500	303	291	287	284	269	229	181	146	112	69

Table 3. Means and 95% confidence intervals for species number in the Mudumalai 50 ha plot (confidence limits were calculated with a t-statistic). The largest quadrat, 1000 x 500 m, is the entire plot, so there were no replicates and thus no confidence limits. The mean number of stems for any quadrat size can be calculated from the mean density per ha over the whole plot: 513.8 for stems >= 10 mm dbh, 472.1 for stems >= 20 mm, 451.4 for stems >= 25.4 mm, 443.0 for stems >= 31.8 mm, 412.3 for stems >= 50 mm, 300.8 for stems >= 100 mm, 177.4 for stems >= 200 mm, 97.6 for stems >= 300 mm, 53.7 for stems >= 400 mm, and 11.2 for stems >= 600 mm. The actual number of stems for 40 x 40 m and 150 x 150 m plots were slightly different, because these quadrat dimensions did not cover the entire 50 ha.

	Size class (mm dbh)									
Quadrat size (m)	>= 10	>= 20	>= 25.4	>= 31.8	>= 50	>= 100	>= 200	>= 300	>= 400	>= 600
20x20	6.8±0.1	6.4±0.1	6.2±0.1	6.1±0.1	5.9±0.1	5.2±0.1	4.0±0.1	2.7±0.1	1.7±0.1	0.4±0.0
25x25	8.6±0.2	8.1±0.2	7.8±0.2	7.8±0.2	7.5±0.2	6.7±0.1	5.2±0.1	3.6±0.1	2.3±0.1	0.6±0.1
40x40	13.1±0.3	12.5±0.3	12.2±0.3	12.1±0.3	11.8±0.3	10.5±0.3	8.4±0.2	6.1±0.2	4.1±0.2	1.4±0.1
50x50	15.6±0.5	15.0±0.4	14.6±0.4	14.5±0.4	14.1±0.4	12.7±0.4	10.3±0.3	7.5±0.3	5.2±0.3	1.9±0.2
100x100	26.2±1.3	25.3±1.2	24.8±1.1	24.6±1.1	24.1±1.0	22.1±0.8	18.3±0.6	14.3±0.7	10.0±0.8	4.6±0.7
150x150	37.1±2.1	35.7±1.9	35.0±1.8	34.8±1.8	34.0±1.6	31.7±1.4	25.8±1.2	20.6±1.3	14.8±1.3	7.6±1.2
200x200	43.9±3.9	42.4±4.1	41.3±3.7	41.0±3.7	40.4±2.8	37.6±2.3	31.2±1.1	25.8±2.1	18.7±2.1	9.9±1.8
250x250	49.9±3.3	47.9±3.8	47.0±3.7	46.8±3.8	46.0±2.7	44.1±1.9	36.6±1.5	30.8±1.6	23.5±2.0	12.4±1.6
500x500	65.0±3.9	63.5±10.8	62.0±13.0	61.0±17.3	60.5±6.9	58.0±2.0	53.5±2.9	46.5±2.2	40.0±0.0	19.5±2.2
1000x1	13.7±0.2	13.0±0.2	12.6±0.2	12.5±0.2	12.1±0.2	10.4±0.2	7.8±0.2	5.3±0.1	3.3±0.1	1.0±0.1
500x2	13.1±0.2	12.5±0.2	12.1±0.2	12.0±0.2	11.6±0.2	10.1±0.2	7.6±0.2	5.2±0.2	3.3±0.1	1.0±0.1
200x2	7.9±0.1	7.4±0.1	7.2±0.1	7.1±0.1	6.8±0.1	5.8±0.1	4.3±0.1	2.8±0.1	1.7±0.1	0.4±0.0
400x4	15.8±0.3	15.0±0.3	14.6±0.3	14.4±0.3	14.0±0.3	12.2±0.3	9.3±0.2	6.5±0.2	4.4±0.2	1.5±0.1
500x5	18.6±0.4	17.8±0.4	17.4±0.3	17.2±0.3	16.8±0.3	14.8±0.3	11.6±0.3	8.4±0.3	5.6±0.2	2.1±0.2
1000x10	31.6±0.9	30.1±0.9	29.5±0.9	29.2±0.8	28.7±0.8	26.0±0.8	21.5±0.7	16.5±0.8	11.5±0.7	5.3±0.5
500x20	29.6±1.0	28.4±1.0	27.8±0.9	27.6±0.8	27.0±0.8	24.6±0.7	20.3±0.7	15.7±0.7	11.2±0.7	5.2±0.5
1000x500	71	69	67	67	66	63	59	52	45	25